THE LARVAL DEVELOPMENT AND ECOLOGY OF THORACO-PHELIA MUCRONATA (TREADWELL)

R. PHILLIPS DALES

Sir John Cass College, London, E. C. 3, England

The Opheliid polychaetes are well known for their localized distribution. Most species are restricted to soils with a relatively narrow range of particle size, some characteristic of fine muds, others of relatively coarse sands. *Thoracophelia mucronata,* like the common species of Ophelia, is found in sands subjected to a relatively heavy wave action, occurring inter-tidally in beaches experiencing fairly heavy surf on the Pacific coast of North America, from Vancouver Island (49° N) to the Punta Banda region, Mexico (31°30′ N). The ecology and life history of such species are particularly interesting, since the larvae, which in all known instances are planktonic, settle on a relatively restricted and unstable substratum.

The development of only one species of Opheliid, *Ophelia bicornis* Savigny, has been worked out in any detail (Wilson, 1948), and although the larval development of *Thoracophelia mucronata* follows a similar plan, there are a number of interesting differences. McConnaughy and Fox (1949) give a brief account of the early development of *Thoracophelia mucronata.* Feeding, and certain aspects of the biochemistry of metabolism, have been studied in this species by Fox, Crane and McConnaughy (1948), and McConnaughy and Fox (1949).

The present study was made over a period of rather less than one year from October, 1950, on the same population studied by Fox and his co-workers at La Jolla, California (32°52′03″ N, 117°15′11″ W).

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Reproduction and Development

The species is dioecious, males and females occurring in approximately equal numbers. Externally alike, they can be distinguished only by the character of the coelomic germ cells. Coelomic oocytes are colorless, biconvex discs 65 μ in diameter, and 25 μ — 30 μ thick at the center (Fig. 1a, a′). The ripe spermatozoon (Fig. 1b) has a dark acrosome, and a tail about 45 μ in length. As in other polychaetes, the spermatozoa arise from "sperm plates" in the coelom. The worms are apparently atoquous, spawning taking place in or on the surface of the sand.

Fertilizations were easily achieved with really ripe gametes, by slitting open the adults and mixing the eggs and sperm in shallow dishes. Surplus sperm could be washed off, and the larvae which eventually swam to the surface transferred to larger vessels.

Development was extremely rapid (at 15° C. — 18° C.), most of the eggs having reached the 16-cell stage within 2 hours after fertilization. Polocytes are large and clearly distinguishable during the early stages of cleavage (Fig. 1c, e, f). The blastomeres of the 4-cell stage are approximately equal in size, so that the direction of rotation of the subsequent cleavage could not be determined merely by inspection. After about six hours an equatorial prototroch has developed, and the young larva swims off the bottom soon afterwards (Fig. 1g). An apical tuft of filaments and a single filament slightly dorsal to the vegetal pole are also distinguishable in the swimming trochophore (Fig. 1g). The larvae at this stage are positively phototactic, and are vigorous swimmers. After about five days the larva (Fig. 2a, a′) has reached a length of about 100 μ, and has become distinctly asymmetrical. The prototroch is more prominent, is composed of several rows of cilia, and completely

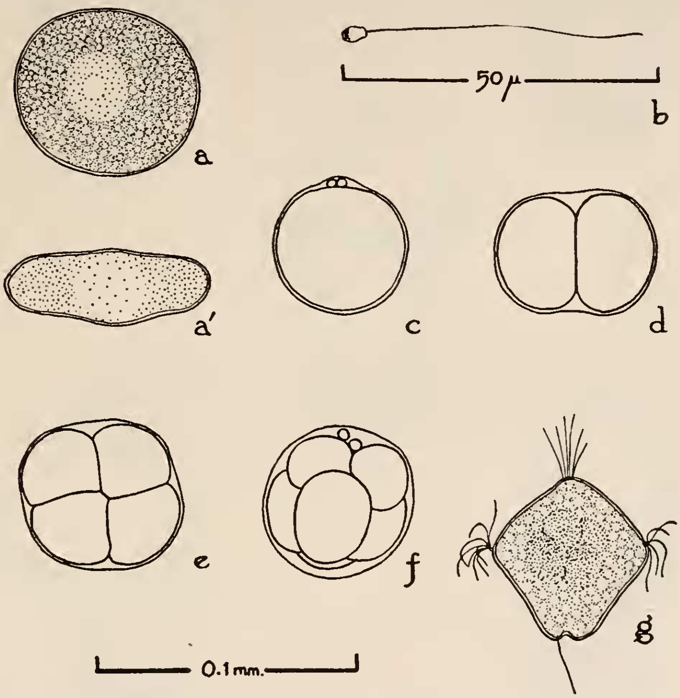

FIGURE 1. Early development. (a), (a′) ripe coelomic oocytes in surface and edge view; (b) spermatozoon; (c) fertilized egg with 2 polocytes; (d) 2-cell stage; (e) 4-cell stage; (f) 8-cell stage; (g) trochophore.

encircles the larva. By this time a telotroch has also appeared, and the mouth and anus have opened into the gut. The anterior apical tuft and the posterior filament remain unchanged until they are lost at metamorphosis.

Throughout the remainder of its planktonic life the larva is markedly asymmetrical, the head region projecting ventrally, forming a large overhanging ciliated lip so that the mouth eventually comes to be directed posteriad, and the stomodeum and the anterior part of the gut are twisted so that the buccal cavity lies slightly to the right, the precursor of the proboscis to the left of the mid-line. Thus at this stage, and in older planktonic larvae, three distinct regions of the gut may be identified:

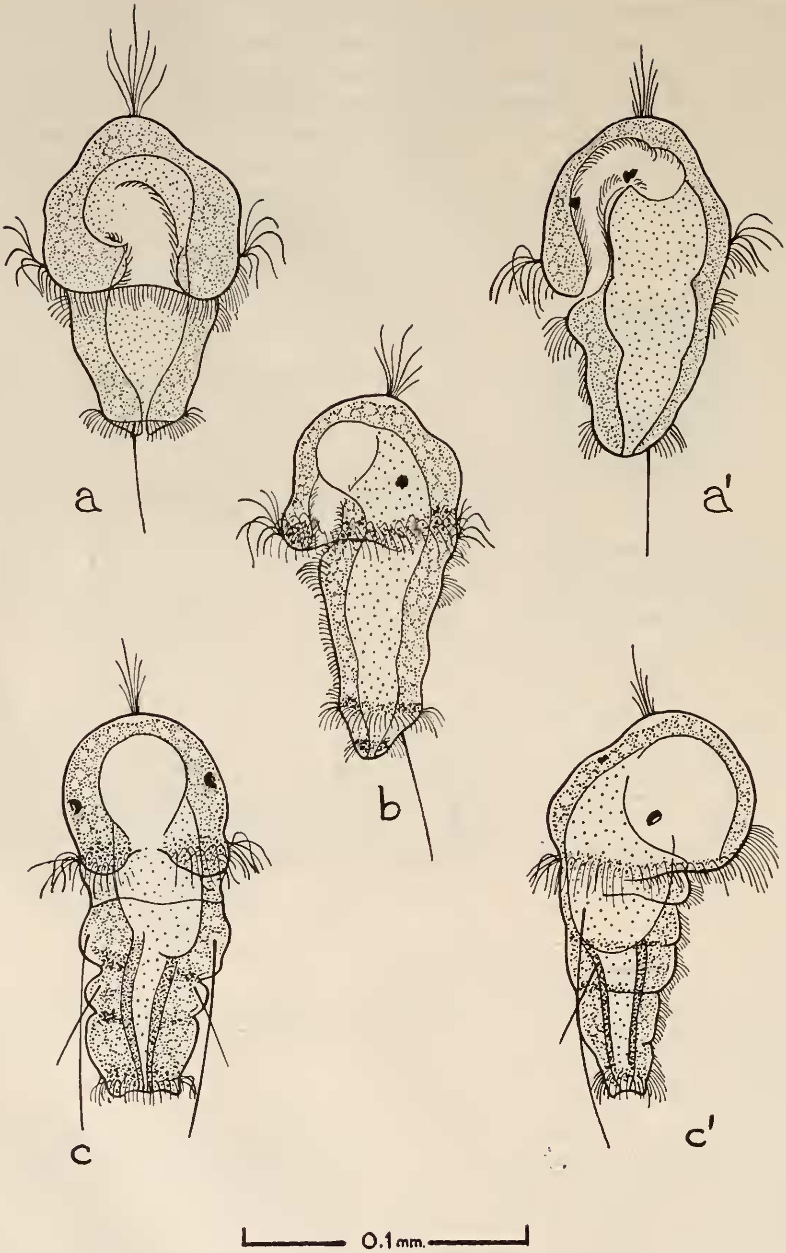

FIGURE 2. Larvae. (a), (a′) 5 days old, ventral view, and view from the left side; (b) 7 days old, view from the left side; (c), (c′) 9 days old, ventral view, and view from the right side.

(1) a ciliated channel opening into (2) a large non-glandular sac, the precursor of the eversible proboscis, and (3) a straight glandular part leading to the anus. Because of the rapid growth of the anterior part of the gut, it becomes not only bent and slightly twisted, but pushed forwards into the prostomium. This condition is apparently only temporary, since young bottom stages (Fig. 3a) show a relatively straight tube leading from mouth to anus.

As will be seen from Figures 2a′, b, c′, additional tufts or short bands of cilia arise from the ventral region of the larva, and in many larvae form a virtually continuous midventral ciliary band. One pair of rather irregular eye-spots has appeared by the fifth day after fertilization, and in later larvae, three or even four eyes may be seen. By the ninth day two chaetigerous segments have been formed, each at first bearing a single chaeta on either side (Fig. 2c, c′). The two pairs of chaetae appear in rapid succession, the anterior pair projecting well beyond the tip of the pygidium when the chaetae are held against the body while swimming. The first chaetae always appear to be simple capillaries, but winged bristles (Fig. 3b) commonly occur in later larvae. When the larva is nine or ten days old, transverse folds in the cuticle appear between the segments. A very definite division appears between the mouth and prototroch, and the first chaetigerous segment. This region just anterior to this groove may represent the first true segment; this problem is discussed below.

By the tenth day slight projections from the corners of the pygidium may be seen, apparently related to the cement glands which by their secretions enable the larva to adhere strongly to the substratum. Although attempts to rear larvae beyond this stage have not been successful, this almost certainly represents the stage of development at which the larva settles out of the plankton and becomes bottom-living. The apical tuft of filaments and the terminal filament are lost, while the pygidial cement glands aid the larva to maintain its position on a suitable substratum when once found. The planktonic life of these larvae is, therefore, probably not more than about ten days. The head is distinctly darker than the rest of the body at this stage. The trilobed proboscis characteristic of the adult is already differentiated in a larva with ten chaetigerous segments, and is eversible by the time the larva has attained a length of 1.0 mm. At this stage the prostomium is still rounded (Fig. 3a) and similar to other Opheliid larvae which have been described, and it is not until the larva is about 2.0 mm. in length that the prostomium has become pointed, and has coalesced with the first two chaetigerous segments (Fig. 4). These segments become cut off from the thoracic region by a transverse septum, the septa between the succeeding segments being absent or ill defined. The sac which opens dorsally through this transverse septum into the anterior or "head" coelom and which extends back to the fifth or sixth chaetigerous segment is already well defined in a young worm 2.5 mm. in length. The whole apparatus is probably an adaptation for burrowing, as McConnaughy and Fox suggest.

The four anal papillae associated with the cement glands (Fig. 3a) are posterior and ventral to the anus. None of these papillae represents the single large ventral cirrus of the adult (as McConnaughy and Fox have stated), since in young worms between two and four millimeters in length the four larval papillae may clearly be seen on the tip of the adult cirrus as it grows out from the pygidium (Fig. 3d). The dorsal cirri are similarly derived from the pygidium, although the last few

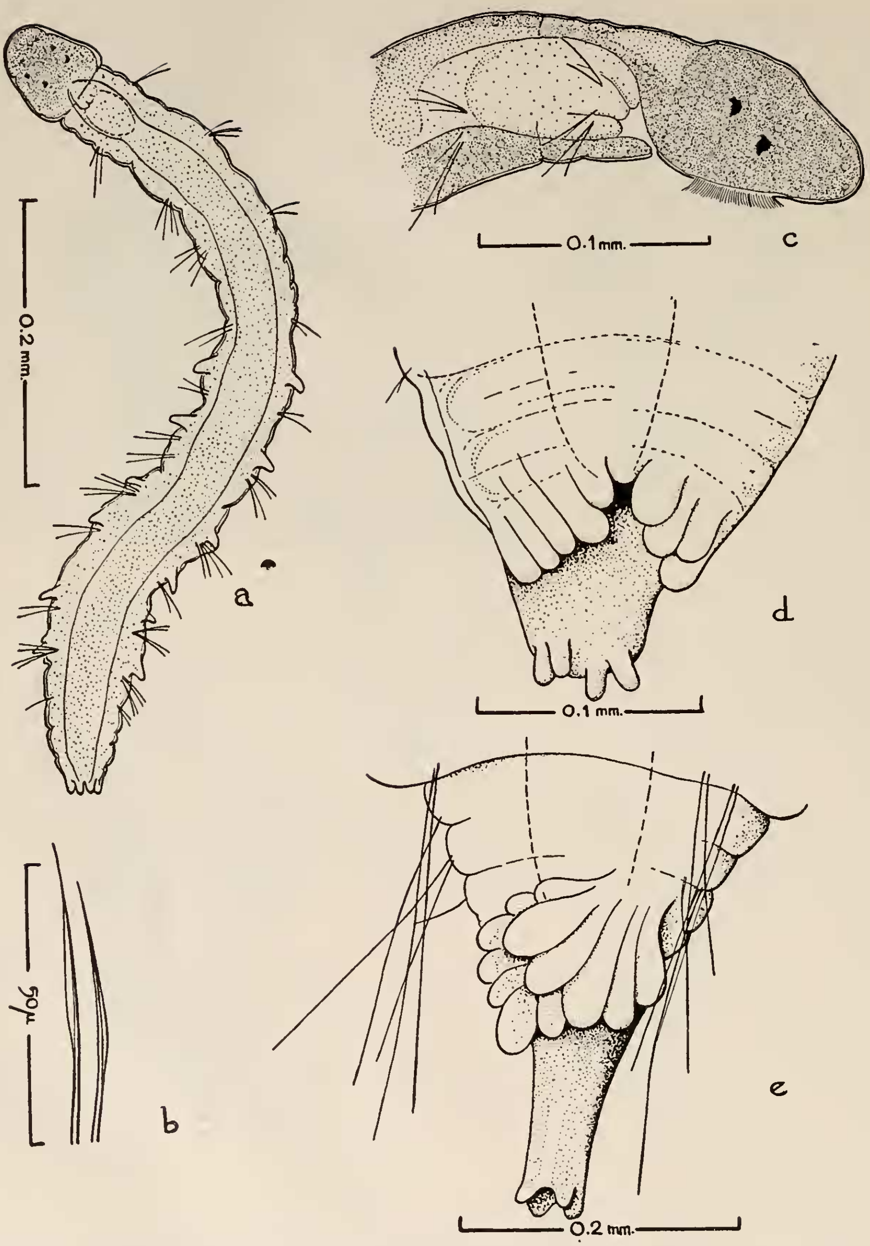

FIGURE 3. (a) Young bottom stage; (b) winged chaetae; (c) side view of the head region of a bottom larva 0.6 mm. long; development of the pygidial region; (d) condition in a young worm with about 26 chaetigerous segments; (e) in a young worm with 36 chaetigerous segments (4 mm. long).

chaetigerous segments become closely associated with it, the chaetae of these segments eventually projecting beyond the anus (Fig. 3e).

Discussion

It is interesting to compare the larval development of *Thoracophelia mucronata* with that of *Ophelia bicornis* as described by Wilson:

Ophelia bicornis	*Thoracophelia mucronata*
Ripe females metallic green in color; males white or pale cream	Ripe males and females similar, the adults containing so much hemoglobin that sexually mature individuals appear only slightly whiter than immature or recently spawned worms
Mature coelomic oocytes oval plates 150 μ × 130 μ	Mature coelomic oocytes biconvex discs 65 μ × 25 μ
Trochophores produced within 24 hours	Trochophores produced within 6 hours

Common features:

Trochophore rounded or slightly conical with an apical tuft, and a single filament projecting from the vegetal pole.

Larva at the time of settling with 2–3 chaetigerous segments; the head rather darker than the rest of the body, and the pygidium with adhesive papillae. Eyespots rather irregular in shape and number. Winged chaetae present.

The eggs are distinctly smaller than those of *Ophelia bicornis* described by Wilson, and this, together with the higher temperatures under which the *Thoracophelia mucronata* normally develops, accounts for the more rapid development in the early stages. Even so, the larvae of *Thoracophelia mucronata* do show a certain acceleration in the development of some structures as compared with *Ophelia bicornis*. The structure of the adult *Thoracophelia* is more specialized than *Ophelia* in the possession of an anterior "head coelom" in relation to burrowing, separated as its name implies from an aseptate "thoracic" region. The proboscis is somewhat precocious in its development, the anterior region of the gut becoming pushed forwards and coiled almost within the prostomial region as already described. Owing to surf action on the shores on which the larvae settle, the early development of burrowing structures would probably be of advantage. The shape of the curve in Figure 5 may also be interpreted as a tendency for a relatively rapid delimitation of segments early in development. It will be seen (Fig. 5) that a *Thoracophelia mucronata* larva has twenty-five chaetigerous segments when 2.0 mm. in length, while *Ophelia bicornis* larvae do not possess this number of segments until they have reached a length of 5.0 mm. By the time young *Thoracophelia mucronata* have reached a length of 5.0 mm. the number of segments usually found in adults (38) has been attained, although old worms may be ten times this length.

Wilson describes in *Ophelia bicornis* the fusion of the first segment with the prostomium, though remaining separated by a groove. The existence of this segment is not clear in *Thoracophelia mucronata,* and is certainly not recognizable in later larvae (Fig. 3a). However, in larvae with two chaetigerous segments there is a clear demarcation between the mouth opening and the first chaetigerous segment (Fig. 2c). It is suggested that this region between the mouth and the first chaetigerous segment represents the first true segment, which in *Ophelia bicornis* is achaetous but distinct, but which in *Thoracophelia mucronata* becomes almost obliterated. That this is likely is shown by the fact that the foregut does develop so far forward as already described, and that the precursor of the eversible proboscis does at first lie anterior to the first chaetigerous segment. Since in most polychaetes the proboscis arises almost entirely within the first segment, it is reasonable to assume that the first chaetigerous segment of *Thoracophelia mucronata* represents the

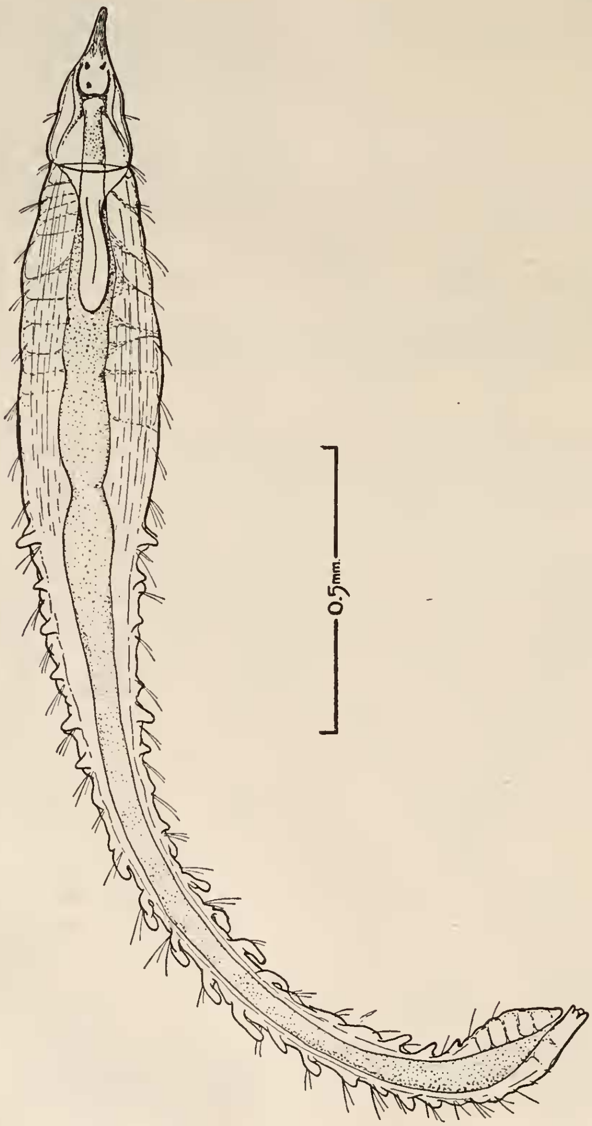

FIGURE 4. Young *Thoracophelia mucronata*

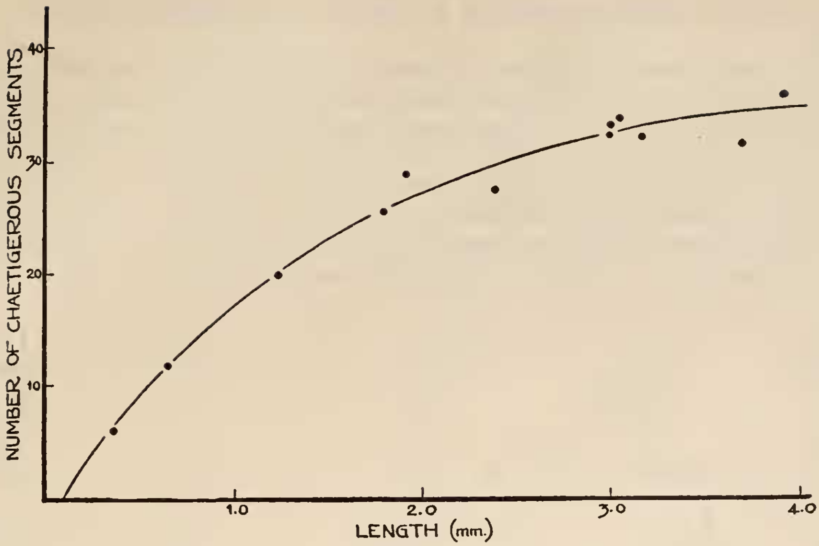

FIGURE 5. Relation of length to number of chaetigerous segments.

second segment, and is homologous with the first chaetigerous segment of *Ophelia bicornis*.

ECOLOGY

The breeding period of *Thoracophelia mucronata* is prolonged during the summer, probably owing indirectly to the equable and relatively high temperatures experienced throughout the year (the temperature of the surface water at high tides varying from a summer maximum of about 22° C. to a winter minimum of about 13° C.). Consequently, the mean length of the worms comprising the population did not vary appreciably from month to month.

Another factor to be considered is the stirring of the surface sand by the surf. Large worms tend to burrow down under such conditions (McConnaughy and Fox, 1949), but a certain proportion are moved after each tide. After rough seas whole areas of the shore normally heavily populated will be depleted of individuals which will be found in immense numbers in channels and pockets where the current loses speed or changes direction. Thus, in spite of the tendency of the larger worms to burrow down, there is an efficient shuffling of the population from time to time, and it is difficult to decide how far the distribution of the worms in the beach is due to purely mechanical agencies. The large amount of hemoglobin which they contain probably acts as an oxygen-store during the periods when the worms burrow deeper to avoid being swept away. When uncovered by the tide, the worms burrow upwards, a small hole appearing on the surface above each worm. This habit is probably respiratory in function, since the worms are usually found head downwards under such conditions, the rectum being used as a kind of lung. The great development of sensory papillae around the anus may thus be understood. The elongate chaetae of the most posterior segments may play some part in breaking the surface and preventing the sand from falling in around the anus while respiration is in progress.

The general pattern of zonation is shown in Figure 6. The six stations were spaced at intervals of about 6 meters between high and low water marks. Samples were taken each month using a square frame with sides 25 cm. in length (enclosing an area of 625 cm.^{2} or $\frac{1}{16}$ m.^{2}), the sample being passed through a sieve with round holes 0.5 mm. in diameter. It will be seen (Fig. 6) that worms extend from low water mark to almost high water mark of ordinary tides, and are not restricted to a relatively narrow belt as McConnaughy and Fox have stated. This belief was due to the restriction of the larger worms to the upper part of the shore, the popu-

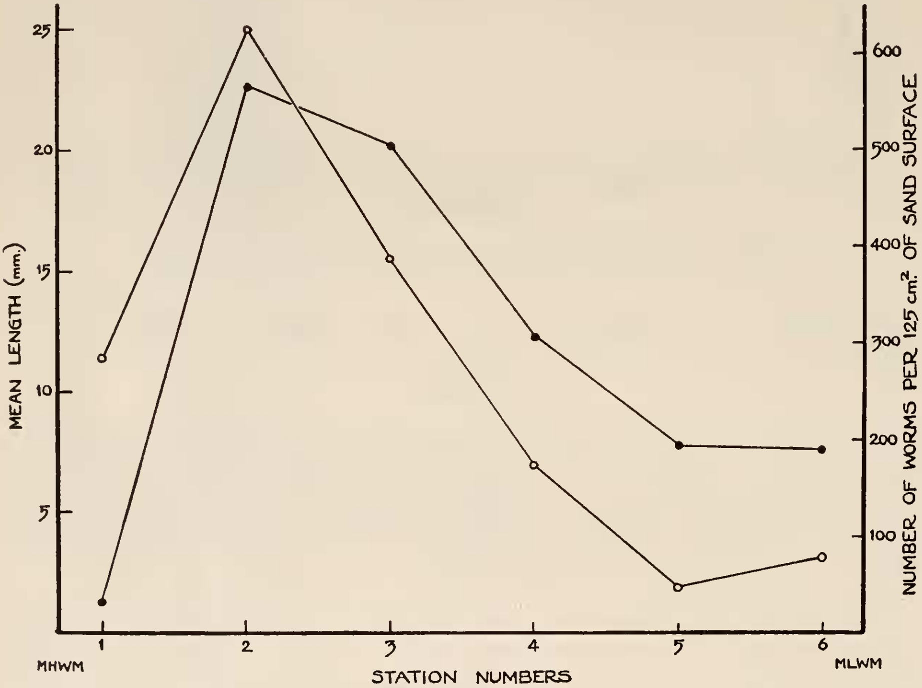

FIGURE 6. Zonation of *Thoracophelia mucronata* at La Jolla. Filled circles = number; empty circles = length.

lation being most dense just above mid-tide level, while the younger worms—which are usually overlooked in the sand owing to their transparency—are restricted almost entirely to the lower part of the shore. A clear division is apparent between the size distribution of worms taken above the mid-tide level where a certain degree of drying out takes place at low tide, and below mid-tide level where the sand remains at or near saturation point (Fig. 7). Two explanations of this division are possible. The larvae may settle over the whole intertidal zone but those above mid-tide level either do not survive owing to the rise in temperature or drying out of the surface sand, or are carried down the beach by the surf. The larger worms are not washed out because of their greater size and weight and ability to burrow be-

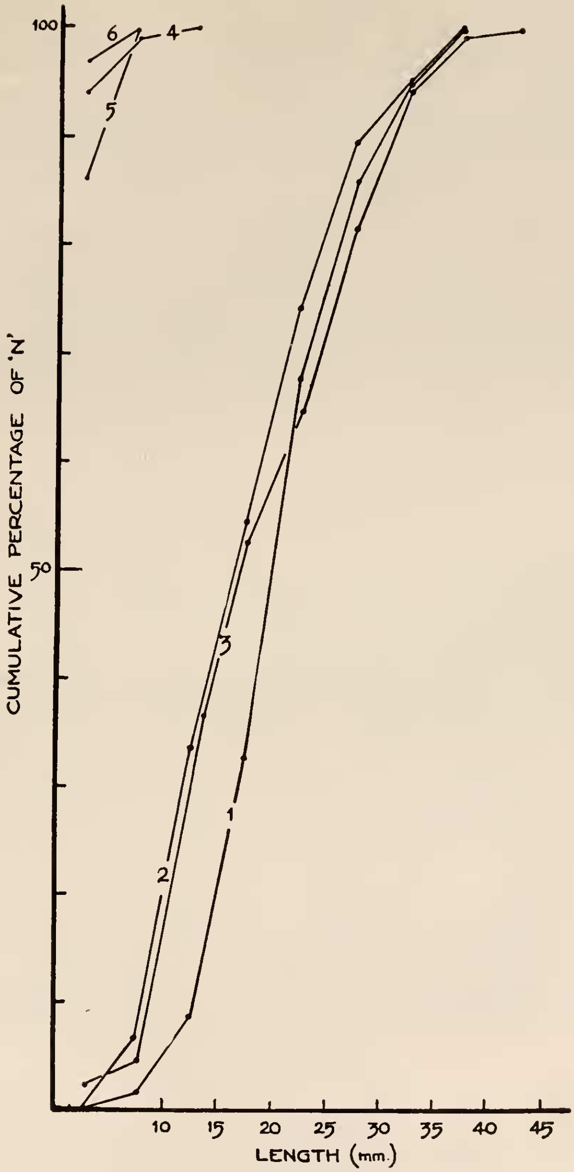

FIGURE 7. Size-distribution of worms at six stations from just below high water mark (1) to just above low water mark (6). Station numbers as in Figure 6.

neath the stirred layer. Secondly, the larvae may settle only below mid-tide level and later migrate upshore. However, it is clear that the optimal zone for the adult worms is appreciably higher than that for the younger stages, but the reason for the relatively sharp division in the mean length of worms from the two zones is not known.

Although there is no doubt that large worms may be redistributed by wave action, under normal conditions there is a certain degree of aggregation as in most polychaetes. The mean density of population at the optimal level was about 10,000–11,000/m.², but within an area of two or three square meters 625 cm.² samples might contain between 500 and 900 individuals (8000–14,000/m.², approximately). Since fully grown worms weigh about 0.04 gm. (McConnaughy and Fox, 1949) and are continually passing sand through the gut, their effect on the mechanical structure of beaches where they occur may be appreciable.

Owing to the large amount of hemoglobin which these worms possess, their food-value for other organisms is considerable, and they constitute an important item in the diet of many shore birds, especially the marbled godwit *Limosa fedoa*.

From a study of the figures obtained from the samples made throughout the year, and from observations made under laboratory conditions, it seems likely that these worms take more than one year to mature, and it is probable that each individual lives for a few years, possibly spawning several times.

Summary

1. The larval development of *Thoracophelia mucronata* follows the same pattern as that of *Ophelia bicornis*, but is much more rapid, the eggs being less than a quarter of the volume of those of *O. bicornis* when mature.

2. The larval development shows differences in the formation of the anterior segments and the anterior regions of the gut.

3. Larvae of both species show the development of the adhesive papillae at the time of settling, and this is regarded as an adaption to settling on an unstable substratum.

4. The great development of hemoglobin in *Thoracophelia mucronata* may be interpreted as an adaptation against surf action, the hemoglobin functioning as an oxygen-store when the stirring of the surface layers of sand causes the worms to burrow more deeply.

5. Attention is drawn to the development of sensory papillae, and the elongated chaetae of the most posterior segments in relation to rectal respiration which is carried on near the surface when the sand is not being disturbed.

6. The optimal tidal level for adult worms is above that of the younger stages; the relation between zonation and the size of the worms is discussed.

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